THE RELATION BETWEEN CHROMOSOME-NUMBER AND SPECIES IN NOTONECTA.[1]

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After working for several years on the spermatogenesis of *Notonecta*, some very interesting facts have recently come to light which I wish to present in a preliminary paper. The material, collected at Woods Hole, consists of three species, *Notonecta undulata* Say, *N. insulata* Kirby and *N. irrorata* Uhler. The character of the chromosome groups is quite distinctive for each species, *N. insulata* representing a transition stage between *N. undulata* with a larger number of chromosomes and *N. irrorata* with a smaller number.

In all three species there is present a pair of idiochromosomes, which divide separately in the first spermatocyte-division, as described by Wilson[2] for *Euchistus*, *Cœnus*, etc. Accordingly, there is one more than the reduced or haploid number in the first division. Owing to the fact that the conjugation of the idiochromosome-pair is often still further delayed in *Notonecta*, the two unequal mates frequently lie side by side on different spindle fibers in the second division (Figs. 7, 9, 16, 18, 33, 35). They subsequently pass to their respective poles without ever having conjugated. As a result of the second division, two classes of cells are produced, one containing the small idiochromosome and the other the large one (Figs. 10, 19, 36). Accordingly, the spermatozoa are of two kinds which, from analogy with other insects, are the male-producing and the female-producing spermatozoa respectively.

In *N. undulata* there are 14 chromosomes in the first spermatocyte-division, consisting of a ring of 12 chromosomes with two small ones in the center (Figs. 1–3). These small ones frequently

[1]I wish to express my thanks to Professor E. B. Wilson for his helpful suggestions and criticism during the course of the work, to the director of the Marine Biological Laboratory and the Wistar Institute of Anatomy for the facilities offered me at Woods Hole, and to Mr. E. P. Van Duzee for identifying the species.

[2]Wilson, E. B., 1905, "Studies on Chromosomes," I., *Journ. Exp. Zoöl.*, II., 3.

give the appearance of being on the same spindle fiber (Fig. 4). There are 13 chromosomes in the second division, a ring of 12 chromosomes surrounding the idiochromosome-pair in the center (Figs. 5–10). The spermatogonial number is 26, including two pairs of small chromosomes, the same ones, evidently, which lie in the center in the first division (Fig. 11).

In *N. irrorata* there are but 13 chromosomes in the first division, a ring of 12 surrounding one small chromosome in the center (Figs. 12–14). In the second division there are 12 chromosomes including the idiochromosome-pair in the center (Figs. 15–19). The spermatogonial number is 24, the smallest pair of chromosomes corresponding to the small chromosome within the ring in the first division (Fig. 20).

In *N. insulata* there are two types of first division groups, occurring in the same testis, in approximately equal numbers. One type has 14 chromosomes, a ring of 12 surrounding two small ones (Figs. 21–23); the other type has but 13 chromosomes, a ring of 12 surrounding only one small one (Figs. 24–26). The apparent discrepancy is accounted for by the fact that the second small chromosome which lies in the center in the 14-group *is frequently found in the 13-group attached to the largest chromosome.* Serial sections of four spindles as seen in side view are given in Figs. 27–30. In the first three series (Figs. 27, 28, 29), there is only one small chromosome in the center of a ring of 12 chromosomes; the second small one is attached to the largest chromosome (*Ma*). In the fourth series (Fig. 30), the two small chromosomes lie free in the center of a ring of 12. A polar view showing the compound character of the large chromosome in the 13-group is given in Fig. 31 (*Ma*). No case of such a compound chromosome has been found associated with the 14-group, and some fifty clear cases have been observed in the 13-group. In many cases, however, the compound nature of the large chromosome could not be determined in the 13-group, the two components having evidently fused beyond recognition. The fusion must take place in all cases before the second division, for there are always, so far as I have observed, 12 chromosomes in this division, including the idiochromosome-pair in the center of the group (Figs. 32–36). All trace of the original composition of

the largest chromosome has been lost. It has a decided quadripartite appearance, as though each element into which it divides were composed of two equal parts. Its appearance suggests that of the large chromosome described by Wilson[1] in the second division of *Nezara*, except that in *Nezara* the two parts are somewhat unequal. Unfortunately, no satisfactory spermatogonial groups have been found, but the expectation would be either 26 or 24, in the latter case, two of them being compound in character.

Discussion.

The chief interest in *Notonecta* lies in the fact that there is a definite relation between the chromosome-number and the species, and that the change in number can be attributed to the behavior of a particular chromosome. In *N. undulata* this chromosome is present as a separate element, together with another small one, in the center of the spindle in the first division, and in the peripheral ring in the second division. In *N. irrorata*, this chromosome is lacking throughout both divisions, there being only one small one in the center of the spindle in the first division. *N. insulata* gives a transition stage between the two; the small chromosome is present in the first division, either free in the center as in *N. undulata*, or fused with the largest chromosome; and it is apparently absent in the second division as in *N. irrorata*. Every chromosome cannot be homologized individually in the three species, for the size relations are different, especially in the case of the idiochromosomes. The largest chromosome and one small one can be followed throughout in the three species. Likewise, we may safely compare, I think, the other small chromosome in *N. undulata* with the one of like size and position that sometimes occurs in *N. insulata* in the first division; and since we can follow the steps of its fusion with the large chromosome in *N. insulata*, we may, I think, reasonably attribute its absence in *N. irrorata* to its permanent fusion with the large chromosome. A schematic representation follows, only the chromosomes that are comparable being separated from the ordinary chromosomes or autosomes, which are designated *A*. The large and small

[1]Wilson, E. B., 1910, "Note on the Chromosomes of *Nezara*," *Science*, May 20, 1910.

idiochromosomes are represented by I and i respectively, the largest chromosome, or macrochromosome by M, the small chromosomes, or small autosomes by a.

	Products of the First Division.	Products of the Second Division.
N. undulata	$M+9A+I+i+a+a$ (14)	$M+9A+I+a+a$ (13) and $M+9A+i+a+a$ (13)
N. insulata	either $M+9A+I+i+a+a$ (14) or $Ma+9A+I+i+a$ (13)	$Ma+9A+I+a$ (12) and $Ma+9A+i+a$ (12)
N. irrorata	$Ma+9A+I+i+a$ (13)	$Ma+9A+I+a$ (12) and $Ma+9A+i+a$ (12)

N. insulata evidently represents a transition stage between *N. undulata* with a larger number of chromosomes and *N. irrorata* with a smaller number. It is not possible to say which is the primitive condition. We might assume that *N. undulata* is the original species, from which, by a process of progressive fusion, have arisen the conditions seen in *N. insulata* and *N. irrorata*. We might, however, assume that the reverse process has taken place; or, that *N. insulata* arose together with one of the other species from the third species.

The somatic characters give no clue as to which of these interpretations should be adopted. We could easily derive the wing coloring of *N. insulata* from that of *N. undulata* by substituting brown pigment for white, and the wing coloring of *N. irrorata* from that of *N. insulata* by substituting black pigment for brown, but leaving some of the brown as mottling. But *N. irrorata* is intermediate in size between the small species *N. undulata* and the large species *N. insulata*. Of course the most striking somatic differences are not necessarily those correlated with the fusion or separation of the two chromosomes; these differences may be correlated with other chromosomes which, as I have stated, differ in size in the three species.

The fact that a transition stage has been found in one species of *Notonecta* between two other species of the same genus in respect to a fusion and separation of two chromosomes lends support to the views advanced regarding the origin of two or more chromosomes from a single chromosome where the transition

stages do not exist. Payne[1] has concluded that the multiple X-element in the Reduviidæ has arisen from a single X-element of an ordinary idiochromosome-pair by a separation into two or more parts. Wilson[2] has accounted for the double accessory in *Syromastes* by assuming that it has arisen from a single chromosome that has split into two parts. These hypotheses are sustained by the evidence of *Notonecta*, two species of which show permanent fusion and separation, and the third species the intermediate condition.

Besides the interesting correlation of the change in chromosome-number and change in species in *Notonecta*, the condition of temporary fusion and separation of two chromosomes in one species, *N. insulata*, is of considerable interest, especially in comparison with the facts found in other insects. Sinéty[3] has found in the Phasmidæ and McClung[4] in other orthoptera that the accessory is sometimes attached to another chromosome; in *Mermeria*, McClung found this compound chromosome further associated with another chromosome. Wilson[5] describes in *Metapodius* a coupling of the supernumeraries with the idiochromosomes during part of the maturation-process. Wallace[6] has found in the spider that the accessory is made up of two components, sometimes united, sometimes separate. Similarly, in *Syromastes*. Wilson[7] has found that the accessory consists of two unequal elements which are closely united in the maturation-divisions. In the Phylloxerans, Morgan[8] describes two accessories, sometimes separate, sometimes united. It is to be noted, however,

[1]Payne, F., 1909, "Some New Types of Chromosome Distribution and Their Relation to Sex," BIOL. BULL., XVI., 3, 4.

[2]Wilson, E. B., 1909, "The Female Chromosome Groups of *Syromastes* and *Pyrrochoris*," BIOL. BULL., XVI., 4.

[3]Sinéty, R. de, 1901, "Recherches sur la Biologie et l'Anatomie des Phasmes," *La Cellule*, XIX.

[4]McClung, C. E., 1905, "The Chromosome Complex of Orthopteran Spermatocytes," BIOL. BULL., IX., 5.

[5]Wilson, E. B., 1909, "Studies on Chromosomes," V., *Journ. Exp. Zoöl.*, VI., 2.

[6]Wallace, L. B., 1909, "The Spermatogenesis of *Agalena nævia*," BIOL. BULL., XVII., 2.

[7]Wilson, E. B., 1909, "Studies on Chromosomes," IV., *Journ. Exp. Zoöl.*, VI., 1.

[8]Morgan, T. H., 1909, "A Biological and Cytological Study of Sex Determination in Phylloxerans and Aphids," *Journ. Exp. Zoöl.*, VII., 2.

that in all these cases, the temporary separation or union is connected with the sex-chromosomes, whereas in *N. insulata* it concerns two ordinary chromosomes or autosomes.

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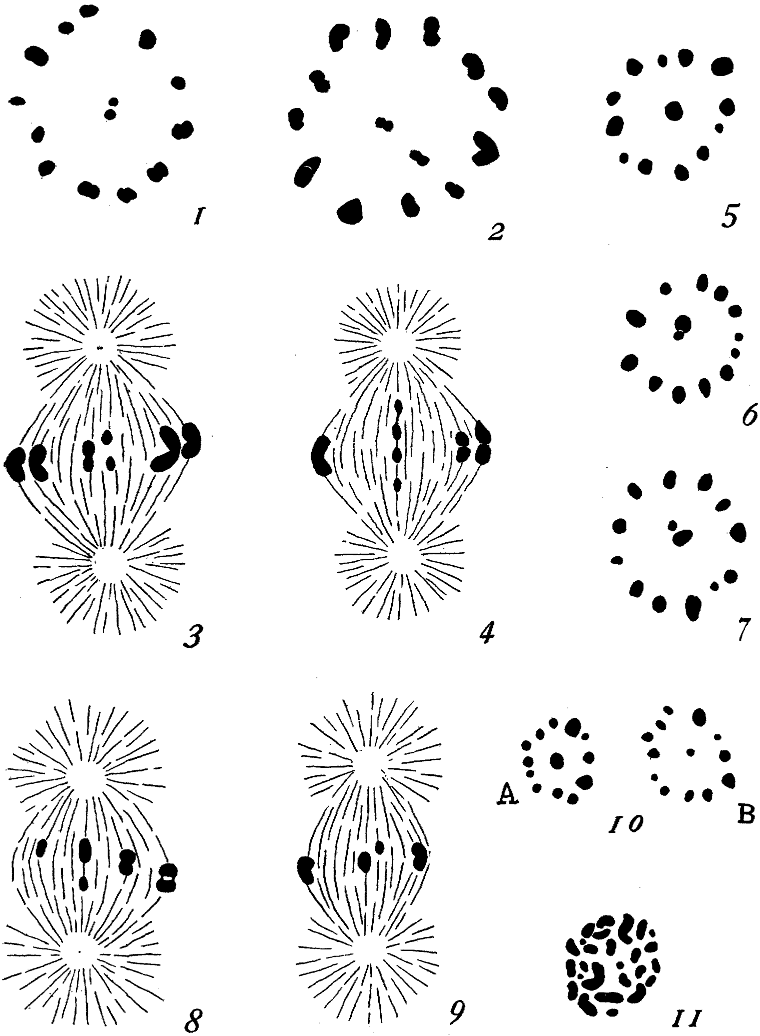
WOODS HOLE, MASS.,
September, 1910.

Explanation of Plate I.

Notonecta undulata. Figs. 1, 2, metaphase of first division showing 14 chromosomes, two small ones in the center. Figs. 3, 4, initial anaphase of first division, side view, two small pairs in the center. Fig. 5, metaphase of second division showing 13 chromosomes, large idiochromosome in the center. Figs. 6, 7, the same, but both idiochrosomes showing in the center. Fig. 8, initial anaphase of second division, side view, idiochromosome-pair in the center. Fig. 9, the same, but idiochromosomes on different fibers. Fig. 10, *A* and *B*, sister anaphase groups of second division, from the same spindle. Fig. 11, spermatogonial group showing 26 chromosomes.

All the figures were drawn with a camera, 1/12 oil immersion and a 12 compensation ocular, then reduced in the engraving to two thirds.



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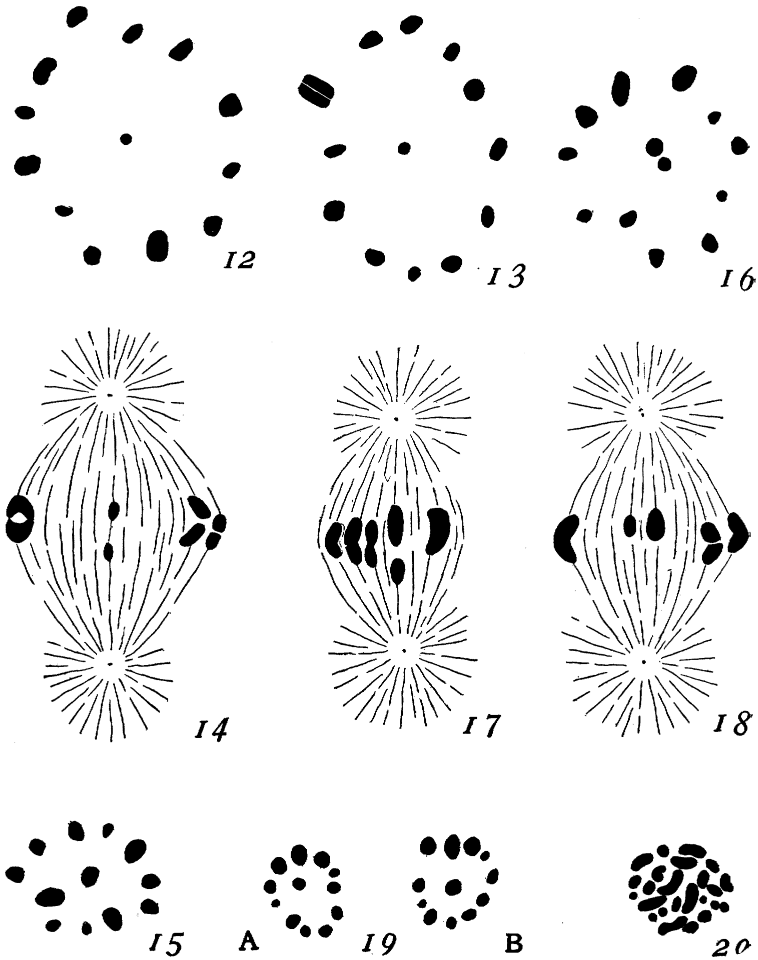
Explanation of Plate II.

Notonecta irrorata. Figs. 12, 13, metaphase of first division showing 13 chromosomes, one small one in the center. Fig. 14, initial anaphase of first division, side view, one small pair in the center. Fig. 15, metaphase of second division showing 12 chromosomes, large idiochromosome in the center. Fig. 16, the same, but both idiochromosomes showing in the center. Fig. 17, initial anaphase of second division, side view, idiochromosome-pair in the center. Fig. 18, the same, but idiochromosomes on different fibers. Fig. 19, *A* and *B*, sister anaphase groups of second division, from the same spindle. Fig. 20, spermatogonial group showing 24 chromosomes.



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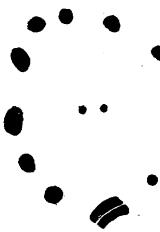
Explanation of Plate III.

Notonecta insulata. Fig. 21, metaphase of first division showing 14 chromosomes, two small ones in the center. Figs. 22, 23, anaphase of first division, side view, two small pairs in the center. Figs. 24, 25, metaphase of first division showing 13 chromosomes, one small one in the center. Fig. 26, initial anaphase of first division, side view, one small pair in the center.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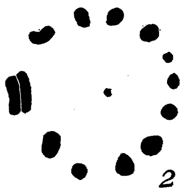
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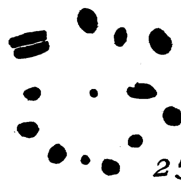
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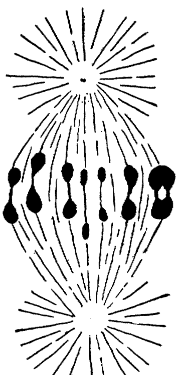
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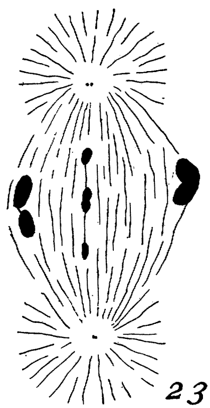
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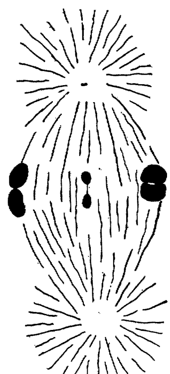
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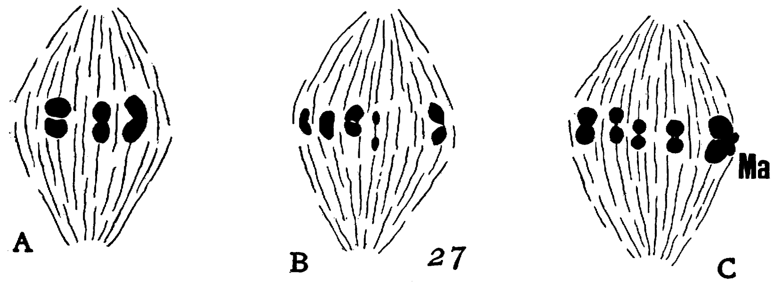
Explanation of Plate IV.

Nonecta insulata. Serial side views of four spindles of first division, as seen in adjacent sections. Figs. 27–29, *A*, *B*, *C*, three entire spindles each showing 13 chromosomes, one small pair free in the center in *B*, and a compound chromosome in *C* (*Ma*) consisting of the large and the other small chromosome united. Fig. 30, *A*, *B*, *C*, entire spindle showing 14 chromosomes, two small pairs free in the center in *B*; the two elements of the compound chromosome are separate as *M* and *a* in *C* and *B*.

Some of the chromosomes have been displaced on the spindles so as to lie side by side instead of one above another, for the sake of clearness.



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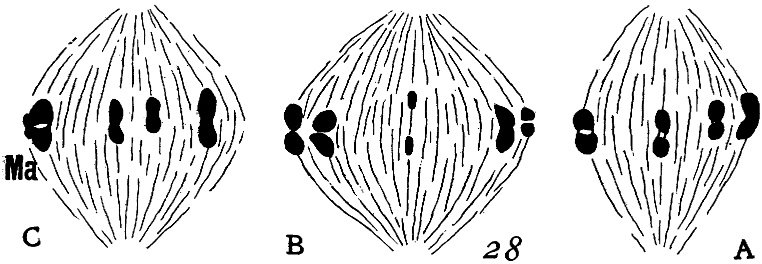

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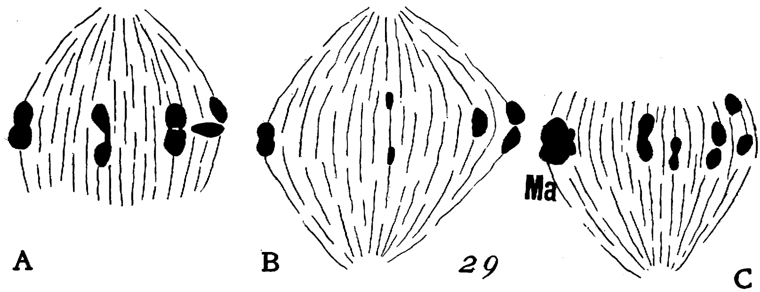

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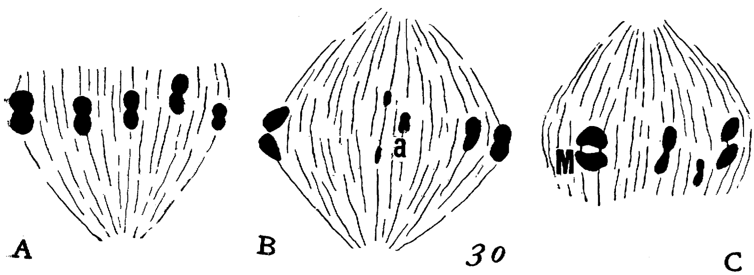

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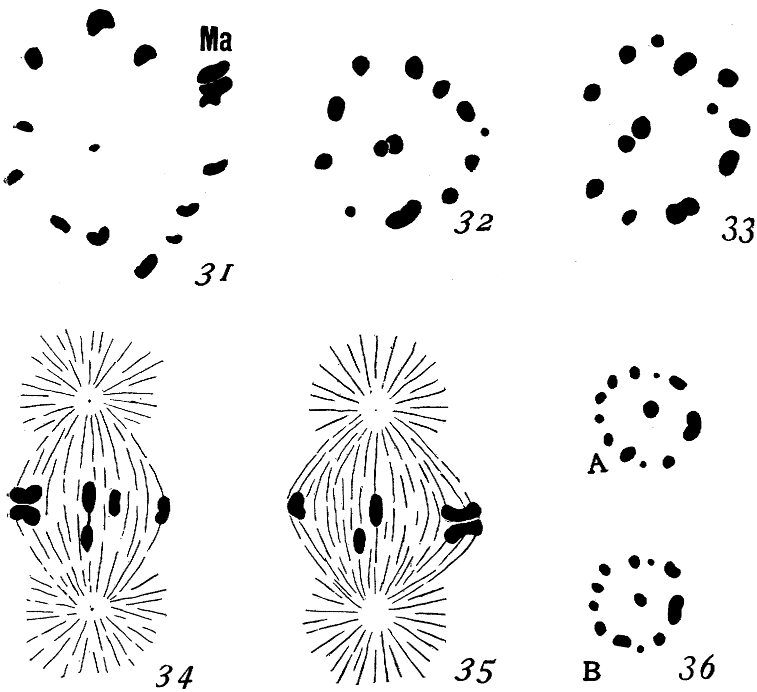
Explanation of Plate V.

Notonecta insulata. Fig. 31, metaphase of first division showing 13 chromosomes, one small one in the center, the other small one attached to the large one forming the compound chromosome *Ma*. Figs. 32, 33, metaphase of second division, showing 12 chromosomes, both idiochromosomes showing in the center, Fig. 34, initial anaphase of second division, side view, idiochromosome pair in the center. Fig. 35, the same, but idiochromosomes on different fibers. Fig. 36, *A* and *B*, sister anaphase groups of second division, from the same spindle.



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